

A NOTE ON THE GERMINATION AND ESTABLISHMENT OF *PHORADENDRON CALIFORNICUM* (VISCACEAE)

JOB KUIJT

Department of Biological Sciences, University of Lethbridge,
Lethbridge, Alberta T1K 3M4, Canada

ABSTRACT

During germination, the radicle of *Phoradendron californicum* elongates greatly, eventually forming a minute disk or wedge from which penetration of the host is effected. Subsequently, the epicotylar pole and the entire radicle wither and die, the young plant having an exclusively endophytic existence for a brief period. All aerial shoots are formed adventitiously from endophytic strands. This pattern of establishment corresponds to that in *Arceuthobium*, but in *Phoradendron* is not known from other species, although a few species in *Phoradendron* and *Viscum* show transitional patterns.

The stage in a mistletoe's life cycle which leads from seed germination to the full establishment of the endophyte is of great biological interest. It is surprising, therefore, that this stage has not been scrutinized in the case of the common desert mistletoe, *Phoradendron californicum* Nutt., even though the interaction of the seedling with its host has received some notice (Cannon 1904; Tinnin et al. 1971). The present note documents some unusual aspects of this early development. Fruits were collected on about 20 May 1982, near Julian, San Diego County, California, the host being *Acacia greggii* A. Gray. The material illustrated in Figure 4 derives from the same locality and host two years earlier.

The most important avian disseminator of *P. californicum* is the Phainopepla, *Phainopepla nitens*, which tends to concentrate eliminated seeds in small clusters on the host branches near the fruiting parasite (Cowles 1936; Crouch 1943). My attention was drawn some years ago to the fact that no erect seedlings could be located even where live host branches were littered with innumerable germinating mistletoe seeds. Furthermore, those seedlings were characterized by an exceedingly long and slender radicle strikingly reminiscent of that of *Arceuthobium* and not at all like the type which one finds in North America and tropical America in other species of *Phoradendron* and in the closely related genus *Dendrophthora* (unpubl. obs.), where radicles tend to be short and the seedlings phanerocotylous. No seedling could be found in which the cotyledons had been withdrawn from the endosperm.

OBSERVATIONS

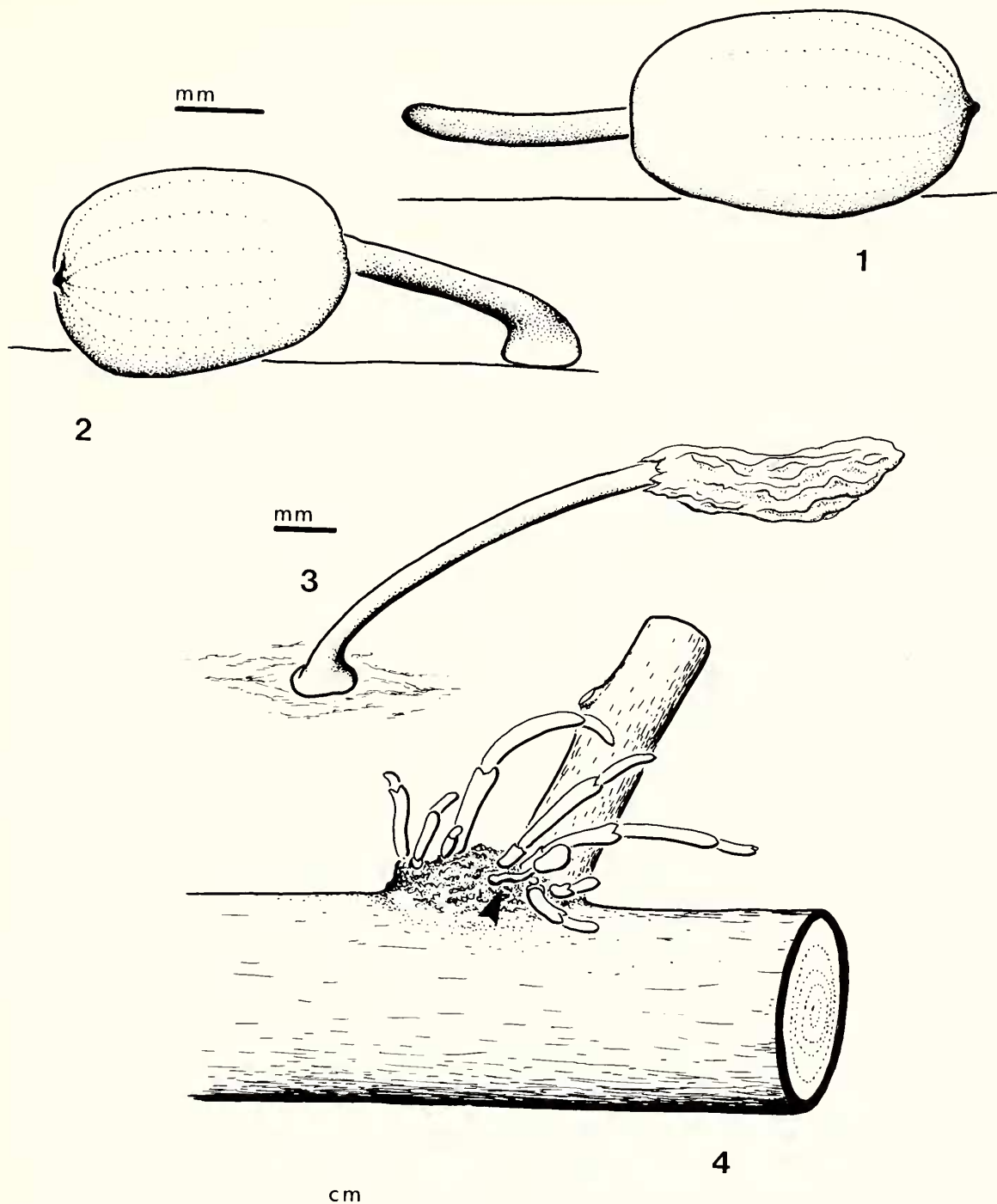
With such questions in mind, I closely followed germination on several potential but unproven host species (*Cassia* sp., *Callistemon* sp., *Nerium oleander* L.) for up to 18 months in the University of Lethbridge greenhouse. Unfortunately, none of the numerous seedlings became established, and the complete transition from the independent stage to parasitic dependence could thus not be followed. Radicles, both in the field and in the greenhouse, are generally bright red and uniformly 0.3 mm in diameter. They often grow out in a nearly straight fashion until about 3 mm long (Fig. 1). Since most seeds become attached to the host in a sideways manner, the initial growth-direction tends to parallel the host surface. Eventually, a hinge-like movement apparently localized just outside the endosperm brings the tip of the rigid radicle into contact with the host, where a disk is formed (Fig. 2). The form of the disk is adapted to whatever space is available at that point, and may thus be more like a flattened wedge or peg. When the seed initially adheres so as to point towards the host, the growth pattern tends to be more regular in that the radicle advances towards the host surface. Conversely, if the seed becomes attached by the end opposite the radicle, the latter curves immediately upon emergence and grows towards the host surface. In one instance, the radicle reached a length of 7 mm and lived for 18 months (Fig. 3), but field conditions probably do not allow such records.

Fortunately, young specimens were collected which unequivocally showed the subsequent development (Fig. 4). The epicotylar end, indeed, does not emerge from the endosperm, and all external portions shrivel up and die after penetration has occurred. In the meantime, the endophytic strands expand into the host tissues and produce a cluster of aerial shoots near the original point of entry. I have no information on how long a period passes before flowering takes place, but I assume this to be not before the second growing season.

In other cases, individual shoots were noted as they emerged from a vigorous endophytic strand visible by a line of raised host bark radiating out from an older plant. The vigor and frequency of shoots which emerge are likely to be a function of the size of the host branch and perhaps host species.

DISCUSSION

The young mistletoe radicle has often been described as being negatively phototropic, thus curving directly towards the host branch no matter on what side it is attached (Kuijt 1969), after which the haustorial disk is formed and the cotyledons and epicotyl are withdrawn from the endosperm. This is undoubtedly true for the great majority of mistletoes (see, for example, Kuijt 1982). It is notewor-



FIGS. 1-3. Germination stages of *Phoradendron californicum*, respectively of the following ages: 1, 1, and 18 months. 1. The radicle has grown out straight, parallel to the host surface. 2. The entire radicle, while still straight, has been lowered, the haustorium forming at the tip. 3. The haustorial disk is attached to the host surface, and the exhausted endosperm has been lifted by the epicotylar pole of the seedling. Germination in greenhouses, University of Lethbridge. 4. The earliest shoots formed of a vigorous, young individual of *P. californicum*, collected on *Acacia greggii*, Julian, California. The original seedling still adheres (arrow) but is dead.

thy, however, that Tubeuf (1923, p. 414) already noted an insensitivity of the radicle to external growth stimuli in the early germination stages of *Viscum album* L., a situation which seems to be comparable to that in *Phoradendron californicum*. Clearly, the rad-

icle passes through physiologically very different stages during germination.

Vegetative reproduction from endophytic strands is common in many Viscaceae, including some other species of *Phoradendron* like *P. villosum* Engelm., some *Viscum* species (Tubeuif 1923; Kuijt 1986) and *Dendrophthora* (Kuijt 1987b), and the entire genus *Arceuthobium* (Kuijt 1960). However, the complete replacement of the normal shoot system derived from the epicotyl by adventitious shoots has not before been reported in *Phoradendron*. This pattern of establishment has earlier been called the *Arceuthobium* pattern (Kuijt 1986), since it has long been known for that genus. It has recently also been shown to occur in *Viscum minimum*, but there appears to be still in a transitional stage from a normal pattern in that the plant does not entirely "withdraw" into the host upon entry, but rather leaves an external haustorial cushion (the disk) from which some of the early aerial shoots are formed (Kuijt 1986). The *Arceuthobium* pattern has evolved independently in a single species of Loranthaceae (*Tristerix aphyllus* (DC.) Barlow & Wiens; Reiche 1904; Mauseth et al. 1985), and is possibly present in *Lepidoceras peruvianum* Kuijt of Eremolepidaceae (Kuijt 1988). It may also be expected in the genus *Phacellaria* (Santalaceae) (Kuijt 1969). This represents at least 3 documented cases of remarkably parallel evolution.

In one group of *Phoradendron* species, all of which are hyperparasitic on other mistletoes, a separate transitional pattern has evolved (Kuijt 1987a). While we do not know anything about the seedlings of this group, it is clear that at an early stage a haustorial cushion is formed very much like that of *Viscum minimum*. It is from this cushion that most (or perhaps all) shoots originate. Whether the primary shoot, and therefore the epicotyl of these species function normally remains to be established. Sprouting from the haustorial disk may, of course, be present in other species as well but is likely to be infrequent. It has not been observed in *P. californicum*.

In summary, then, I have shown that the seedling of *P. californicum* is cryptocotylar and of the *Arceuthobium*-type of development in that all aerial shoots are adventitious, the primary apical shoot meristem aborting. The "seed coat" of this mistletoe forms a shiny capsule around the living endosperm, and it is worth mentioning that the only North American member of Loranthaceae s.s. to become similarly adapted to deserts, *Psittacanthus sonora* (S. Watson) Kuijt, has evolved a comparable sheathing capsule and cryptocotylar germination pattern (Kuijt 1973). In fact, these two mistletoes in Baja California may be found together and even in hyperparasitic combination (Kuijt 1971). The above-mentioned *Viscum minimum* also is a distinctively xeric species, being parasitic upon extremely succulent *Euphorbia* species in South Africa, as is *Tristerix aphyllus*

on several desert cacti in Chile. The desert environment thus seems to have brought about parallelisms in the pattern of establishment of diverse mistletoes. The germination pattern in *Arceuthobium*, similarly, may point to an early evolutionary origin in a desert environment.

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